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THE NATURAL HISTORY, ORGANIZATION AND LATE DEVELOPMENT OF THE TEREDINIDAE

DISSERTATION SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS
UNIVERSITY IN CONFORMITY WITH THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

BY

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by shipping in modern times. It was Godfrey Sellius who first recognized the Molluscan characters of *Teredo*, but these were not used by Linnaeus, who grouped it along with *Serpula* and *Dentalium*. Cuvier and Lamarck adopted the view of Sellius, and since their time the group has been put in its proper place.

The first reliable observations on the anatomy of the "ship-worms" were those of Deshayes, who gave a number of beautifully executed plates to *Teredo* in his "Mollusques d'Algerie," 1846. However, like most of the plates of this great work, they are difficult to study and interpret. Supplementing the work of Deshayes is that of Quatrefages, (14) who began and completed his observations before he had access to the published results of Deshayes. This "Memoire sur le Genre Taret (*Teredo*, Linn.)" is the one usually cited at the present time, although the paragraph with which Quatrefages prefaces his paper is almost as applicable now (with slight changes in the wording) as when it was written in 1849. "Naturalists up to the present time," he says, "have strangely neglected *Teredo*. This is not the place to review the anatomical researches of the last century which are filled with errors excusable by the state of science of that period. But it is surprising that a mollusc with such remarkable external characters has not been the object of any special research from the foundation of comparative anatomy up to the present time. It is necessary to come to the year 1846 to find a naturalist who has taken for the subject of his observations this mollusc so unfortunately celebrated.

Since the appearance of the memoir of Quatrefages, no detailed account of the whole organization of *Teredo* has appeared. Only in comparative treatises has it been taken up. The principal of these are the papers by Grobben (4) on the pericardial glands in Lamellibranchs, by Menegaux (11) on the circulatory system in Lamellibranchs; and by Pelseneer (14) in his extensive comparative studies in the group.

Grobber first observed the anterior adductor muscle in *Teredo* and proved the *Tereidinidae* to be *dimyarians*. Aside from this point, the figure of *Teredo* that he gives is wholly unreliable. Menegaux attempted to establish the homologies of the aortae, and Pelseneer described the visceral ganglion and related structures. I shall have occasion to refer to these papers in special parts later, and it will be seen that the comparative method of study is not always satisfactory, if the examination of special forms be not made with sufficient care. My results differ from all of these. Unfortunately the first two do not state the species on which they worked, and so I cannot state that where my observations differ from theirs, they were in error, though there is such great uniformity of organization in the various species, that we may expect only differences in detail in the various types.

My observations have been based chiefly on *Xylatrya fimbriata*, Jeffreys, and unless otherwise stated, this is the form described and figured. Specimens of this species I have had in all stages of development from the newly attached larva to the adult. I have also studied *Teredo norvegica*, Spengler, and *T. navalis*, Linne and where these are essentially different or more favorable for description, they have been used. In general, where "*Teredo*" is used as a popular term, it applies to *Xylatrya* as well as to the species of *Teredo*, in a strict sense.

The object of my study of the "ship-worms" has been twofold. In the first place, I have endeavored, by the use of modern methods, to give a detailed account of the organization of this highly specialized Lamellibranch and to correct the errors that have heretofore existed in the descriptions of it. In the second place, by the study of young stages, I have been able to trace the transformation of the typical Lamellibranch larva into the highly specialized "ship-worm."

I have also traced the early embryology on the artificially fertilized eggs of *X. fimbriata* and *T. norvegica*, in both of which the eggs are laid free into the water. Stages later than

the typical Lamellibranch veliger raised in aquaria, I have not been able to observe. The intermediate stages, between these and the newly-attached larva, I hope to observe on the larvae of some viviparous species at a future time, so as to complete my study of the development from the egg to the adult.

II. METHODS.

My preserved material was collected and prepared for study as follows: By hanging boxes and other structures of wood in the water at Beaufort, I was able to obtain all stages from the newly-attached larva to "ship-worms" four inches long, with adult organization. The youngest stages were collected from the surface of the wood. Later stages were dissected out of the wood into which they had bored. Early stages were narcotized with cocain and afterwards fixed with mercuric chloride. Specimens 1 cm. or more in length were treated as follows: They were exposed quickly and immediately a quantity of Hermann's solution was dashed upon them. This kills them instantly, before they have had time to contract appreciably. They were then immediately immersed in mercuric chloride or Perenyis' solution for fixation. After washing in weaker alcohols, specimens were preserved in 90 per cent. alcohol. The early stages were stained in Kleinenberg's hematoxylin. For later stages, the best results were obtained with borax-carmines, followed by Lyons blue. For the examination of whole objects, the best results were obtained by staining in a weak solution of borax-carmines in acid ($\frac{1}{2}$ per cent. HCl.) 70 per cent. alcohol, which decalcifies as well as stains. The figures have all been drawn with the aid of a Zeiss camera lucida. In some cases, as in the series of transverse sections of the adult, they have been "touched up" afterwards. However, in no case have they been essentially modified and are in no wise diagrams. The figures of adults have been made from specimens about ten centimeters long, which I had raised, and which were killed perfectly extended. The siphons, however, have been filled in from life, or from pre-

served specimens that had been narcotized before killing. In larger specimens the body as a whole, and the various organs are somewhat more elongated, but the relations remain the same as in younger specimens.

III. NATURAL HISTORY OF THE "SHIP-WORMS."

Any wooden structures that one may examine at Beaufort, which have been in the water for some time and unprotected, are always found infested with "ship-worms." These are of three species, which Professor W. H. Dall has kindly identified for me as *Xylotrya fimbriata*, Jeffreys, *Teredo navalis*, Linne and *T. norvegica*, Spengler. *X. fimbriata* and *T. norvegica* are very abundant, while *T. navalis* is found but rarely. *X. fimbriata* is the most abundant of all, and is found everywhere. It may attain a length of two feet, though where it grows in large numbers it is so crowded that specimens are oftener less than a foot in length. *T. norvegica* I have found mostly in the heavier piles of wharves, where specimens may attain the great size of four feet in length and an inch in diameter. *T. navalis* I have found very sparingly, not over a dozen specimens among the thousands of individuals I have examined. These in all cases were small specimens, from which it seems that the habitat at Beaufort is not favorable for them, and is more favorable for the other two species which fully occupy all of the available places for "ship-worm" life. The water contains a high percentage of salt, and the warm season is long, and these factors may account wholly or in part for the absence of *T. navalis*.

Of the thousands of young specimens (under four inches in length) I have taken from boxes, all were of *X. fimbriata* except four specimens of *T. navalis*. These were observed in June, July and early in August. Whether the absence of *T. norvegica* was due to unfavorable locations, or the season for attachment is different from that of the other two species, I was not able to determine.

BREEDING HABITS.—As is well known, some species of

Teredo retain their eggs in the gills during the embryonic development. This is true of *T. navalis*, and even the small, (an inch or more) specimens of this species I have taken, have usually had embryos in various stages of development. On the other hand, I have found that the eggs of the other two species are laid free into the water. If species of *T. norvegica* be taken from their tubes, they soon begin to extrude their sexual products, if these be mature. The eggs and sperm are extruded from the anal or exhalant siphon in a slow, steady stream, which continues as long as the sexual organ contains ripe sexual products. *Xylotrya fimbriata* I have observed but rarely extruding its sexual products in this manner, but why there is a difference in this habit I have not determined.

In accordance with their free development in the water, the eggs of the "ship-worm" are very small and very numerous. While they vary somewhat in size, they have an average diameter of somewhat less than 1-20 mm. Very large specimens may lay great numbers of eggs at one time; in one case I estimated the number laid by a large female of *T. norvegica* at one hundred million. The sperms are very minute, and much more numerous than the eggs. The eggs of both species that lay their eggs free may be fertilized artificially, and pass the early stages of development with great uniformity and rapidity in aquaria. The eggs when first laid are of irregular shapes. They soon become spherical, and if fertilized, the polar bodies are soon extruded and segmentation begins. Development is very rapid and on warm days, the embryos become free-swimming within three hours after the eggs are laid. Within a day the shell has been formed and the typical Lamellibranch veliger stage is reached. Beyond this stage they do not develop in aquaria, though they may live for days afterwards. Hatschek has observed (6) that the Viviparous larvae of a species studied by him (*T. navalis*?) are almost always present in only a few stages, and that transitional stages are but seldom found. It seems probable that the free-living larvae of *Xylotrya* and *T. norvegica* attain one of these stages within

a short time, and that the unusual conditions in aquaria prevent their advance beyond it.

The mode of life, and rate of development beyond the early stage attained so rapidly in aquaria, have not been determined. What becomes of the larvae that hatch from the eggs, how and where they live, it is difficult to surmise. Though the developed larvae are settling on wooden structures constantly, I have not taken them and intermediate stages in the tow-net, and where they develop I do not know. However, the rate of growth of the marine Lamellibranchs is slow, and I think the larvae of "ship-worms" that attach must be at least a month old, it may be more. At this time their development is quite advanced and their organization complex.

The breeding season of *X. fimbriata* and *T. norvegica* seems to extend through the warm season. I have found ripe sexual products of both species from early in May till the middle of August. At the latter time there seemed no abatement in their development. As will be described later, individuals became sexually mature in a month after they have attached, and those which attach in August must bear ripe sexual products later in the season, so that the breeding season seems to extend through the summer.

ATTACHMENT OF THE LARVA.—During its free mode of life, ✓ the "ship-worm" larva has gradually developed into the typical larva of marine Lamellibranchs. There is a shell into which the whole creature may be withdrawn for protection; a large swimming organ, the velum, by means of which the larva swims freely in the water; a long, active foot, by means of which it crawls actively over surfaces. At the end of this larval development, in fact, the "ship-worm" larva is a typical small bivalve, except that it possesses the swimming organ.

Throughout the summer (or at least from May till August) at Beaufort, if one examines unprotected wooden structures submerged in the water, very small bivalves will be found crawling actively over the surfaces. These are very minute and are

easily recognized as "ship-worm" larvae what have just settled upon the wood. The larva moves rapidly in search of a favorable place for attachment, and this is usually in some minute depression or crevice in the wood, though it may also become attached to perfectly smooth surfaces. It seems to possess no organ of special sense for the purpose, and yet, it is able to determine what places are favorable for its future life, and to avoid those which are not. Once it has chosen a point for attachment, it throws out a single long byssus thread, which secures it at the surface of the wood, and soon loses its velum, so that it can no longer lead a free life. Once attached, the larva begins to clear away a place, by scraping away the surface of the wood with the ventral edges of its shell valves. Small particles of wood and other substances that are thus formed, are cemented together over the larva so as to form a sort of conical covering for protection. This formed, the transformation of the larva into the small "ship-worm" begins and progresses rapidly. The foot becomes a pestle-shaped organ which assists the shell in burrowing. The shell valves lose their power of opening at the ventral side, and by the development of knobs on the ventral and dorsal portions of either valve, they are able to swing on each other at right angles to the former direction. Meanwhile the shell gapes at both anterior and posterior ends, for the protrusion of the foot in front, and the siphons, and later the body, behind. And on the anterior edges have been formed the small teeth which at this and later stages are the mechanical agents by which their possessor bores into the wood. This transformation has taken place within two days from the time the larva has settled, and afterwards the animal rapidly becomes a "ship-worm," enlarging its burrow in the wood as it increases in size.

RATE OF GROWTH WITHIN THE WOOD.—The "ship-worm" ✓
in its larval stages develops but slowly, but once in the wood, it grows with remarkable rapidity. During its free life, most of its energies seem devoted to active locomotion and develop-

ment; after attachment, it leads a sedentary life and its growth is correspondingly rapid. The newly-attached larva is somewhat less than .25 mm. long. In 12 days it has attained a length of about 3 mm.; 16 days, 6 mm.; 20 days, 11 mm.; 30 days, 63 mm., and 36 days, 100 mm. It is thus seen that within two weeks from the time it has settled, the "ship-worm" has increased hundreds of times in size, and in five weeks, thousands of times. Within two weeks it has changed to a real "ship-worm," and even in a month specimens may contain ripe sexual elements, though normally these are retained till larger quantities of sperm and eggs are stored for extrusion at one time. I shall describe later what appears to be a change of sex from males to females, the male sex being developed in young specimens. I have found males four weeks old gorged with ripe sperms, and in every way adult.

The ages of larger specimens I have been able only to estimate, from the time the piles and other wooden structures from which they were taken, had been in the water. In one case I took specimens four feet long and an inch in diameter at the anterior end, from piles that had been in the water less than two years. This was in July, and in this case it seems the "worms" had entered the wood not earlier than the spring of the preceding year, and hence were little if any over a year old.

The rate of growth seems to depend but little, if at all, on the hardness or kind of wood. It is well known, "ship-worms" penetrate all kinds of wood, whether it be soft white pine or hard oak. In India there are types that bore into stiff clay. None of our species adopt such a habitat, so far as I know. But I have found small, abnormal specimens of *Xylotrya* in very rotten wood, and I take it that their abnormal character was due to unusual conditions. In this case they were associated with *Xylophaga dorsalis* and *Pholas dactylus*. However, in wood proper, I have observed that they grow quite as rapidly in hard yellow pine as in soft white pine; so that the rate of growth seems conditioned by food supply, and not by the ability of the animal to form its burrow.

PROTECTIVE ADAPTATIONS.—The life of the “ship-worm” in the wood has led to profound changes in the character of its external parts and its means of protection. As the “worm” enters, the posterior part of the body projects more and more beyond the shell which loses its protective character, to take upon itself the sole purpose of burrowing. In specimens 2 mm. long, the shell is still a quarter of the length; in specimens four feet long, the shell is an inch or less in length. With the loss of protection by the shell, other means are acquired. In a general way, the burrow offers the protection afforded by the shell in other forms. But the very delicate tissues of the mantle would be injured by the rough surface of the wood, and so as the body elongates, it secretes around it a constantly thickening calcareous tube, which lines the whole burrow except the anterior end, where the mantle is somewhat less delicate; and where the tube fades out and the burrow is being constantly enlarged.

When the young “worm” enters the wood, it penetrates vertically to the surface, but soon bends its course, so that within two inches, usually, it becomes straight and the worm bores with the grain. Individuals that enter the wood on end, cut across the grain from the start, so that their burrows are straight, unless they are turned from their course by obstructions of any sort. If these are met, the course is changed so that the burrows may become very tortuous. When the “ship-worm” is in danger of boring into the tubes of its fellows, or into other spaces, if its course can be no longer changed, it contracts the anterior part of the body slightly, secretes a closed calcareous lining in front of it, and ceases to burrow further and to grow. Otherwise, it seems it may grow indefinitely, and it is difficult to predict how large specimens of *T. norvegica* might become, were there not adverse conditions to stop their growth.

I believe the calcareous lining of the burrow has been acquired primarily for the protection of the very delicate body from the rough surfaces of the wood. But it serves other purposes also. It prevents the diffusion of injurious substances into the burrow, and also prevents the intrusion of other creatures that live in the wood. Then, too, when the surrounding wood decays, or is eaten away by other animals, so as to endanger the life of the "ship-worm," the tube may be so strengthened as to serve as the sole means of external protection. In this way the walls of tubes which, protected, are usually not over a quarter to a half millimeter thick, may become two millimeters or more thick. This response of the animal to changed conditions on the outside is a very mysterious one and it is difficult to see by what means it recognizes its danger.

The peculiar mode of life of *Teredo* has led to the development of the palettes. These are protective structures peculiar to the "ship-worms." They differ somewhat in the various species, but are essentially calcareous paddles, attached one on either side of the posterior end of the body. In *Xylotrya* the paddle part consists of a series of funnel-shaped calcareous structures, set one within the other upon a cylindrical handle. while in *Teredo* it is composed of a single piece. The handle of the paddle is imbedded in an invagination of the mantle and the paddles project freely behind, where by means of a set of muscles, they may be protracted forcibly so as to completely close the outer end of the burrow, against the intrusion of any enemy from the outside. Also, when the burrow extends upwards and is more or less exposed at low tide, the palettes may so hermetically close the external opening as to retain the water in the burrow, and to prevent the collapse of the body of the "ship-worms." When the animal is feeding, the palettes are drawn forwards and the siphons are extended freely into the water. When it is disturbed in any way, the siphons are contracted very quickly and the palettes forced into the end of the tube.

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MODE OF BURROWING.—The manner of mechanical formation of the burrow has been one of the most debated questions in the natural history of the “ship-worms” and their allies. In *Teredo*, various structures have had this work assigned to them, by various observers. In some cases the observers thought that some chemical solvent assists the mechanical action by softening the wood. Hancock thought there were siliceous particles in the mantle, to do the work. He probably observed the teeth as yet unattached to the shell. Quatrefages thought it the “cephalic hood,” aided by some chemical solvent. This structure he described as muscular, though it is but little muscular and could do no such important work as he assigned to it. Jeffreys thought it the foot, which by other observers was described as wholly absent. Osler, in 1826, had suspected the real mode of formation, though he did not actually observe it. The shell is the agent, assisted by the foot, as I have actually observed in young specimens under the microscope. The whole structure of the shell and the arrangement of its adductor muscles indicates this mode. The teeth on the anterior edges of the valves point outwards and backwards. On both dorsal and ventral portions of each valve there are stout calcareous knobs, which form a double pivot by which the valves swing upon each other, by the contraction of the adductor muscles. The mode of burrowing is as follows: While the foot performs a cupping action, so as to draw the shell close against the surface of the wood, the posterior adductor muscle contracts, so that the teeth on the shell rasp away the wood. The valves are brought to the original position by the small adductor. The comparatively very large posterior adductor is therefore the active agent that does the work, aided by the foot; the shell is the tool by which it is done.

✓
INGESTION OF WOOD AND FOOD.—As in other Lamelli-
branches, a constant stream of water is passing through the siphons when they are extended into the water, which serves for

respiration and also contains the small organisms which serve for food. These consist mainly of diatoms and simple floating algae, and other minute organisms. Small crustacea and other animal forms seem almost never eaten.

The particles of wood that are rasped away in forming the burrow are ingested, as the only means of getting rid of them. It has often been debated whether they undergo any digestion in the alimentary canal, and I am inclined to think they contribute something to the nutrition of "ship-worms." Boring I think to be a periodical function, perhaps alternating with more active ingestion of food. This is indicated by two facts. In the first place it seems that while the teeth are being cemented to the anterior edges of the valves, the shell could not be used. Also, the caecum of the stomach contains mainly particles of wood, which indicates that while burrowing, the orifice into it is open. The caecum contains a very large fold of the internal membrane and seems so eminently an absorbent structure, that for this reason it seems to me there must be some action on the particles of wood within it.

IV. ORGANIZATION AND LATE DEVELOPMENT OF THE "SHIP-WORMS."

(a). THE GENERAL ORGANIZATION.

In their form and general organization, the adult "ship-worms" are the most peculiar and striking of all the Lamellibranchs. Their newly-attached larvae have the form and most of the organization of the larvae typical of most of the marine Lamellibranchs, which are free-swimming during their larval development. The transformation of the typical larva into the highly specialized "ship-worm" takes place with such great rapidity as to properly be called a metamorphosis.

THE LARVA AND ITS METAMORPHOSIS.—The general shape of the newly-attached larva is that of a small clam, with equal shell valves. These latter are broader than long, so that this Lamellibranch which has a more elongated adult, has a larva more fore-shortened perhaps, than any other form. The youngest specimens I have found were creeping over the surface of the wood by means of their very active, tongue-shaped foot. The velum was in all cases retracted into the large velar cavity, a large space in the anterior, dorsal part of the shell cavity. The foot at this stage is very long, ciliated over most of its extent, and angular at its posterior end. This angular portion is occupied by a well developed, though simple byssus apparatus, which throws out a single, simple byssus thread, several times as long as the diameter of the larva. This serves to secure the larva in the early stages of attachment, so that, after the velum has been lost, it may still return to its moorings if it lose its footing from any cause.

The siphons are already well developed in the larva, the ventral with ciliated sensory papillae, the dorsal, a simple non-ciliated tube. The gills have advanced but little beyond the stage figured by Hatschek (6) for the viviparous larva studied by him. On each side of the body there are two large gill-slits, and in the gill membrane, the rudiment of a third. The "ship-worm" larva is a typical dimyarian. Both adductor muscles are present in their usual positions, the posterior already larger than the anterior. The retractors of the foot at this stage are attached in the unbonal region of the shell just in front of the posterior adductor.

The alimentary canal is already highly specialized. A comparatively long oesophagus leads into the stomach, from which a single large liver vesicle projects on either side. The sheath of the crystalline style projects from the posterior ventral portion of the stomach on the midline. The intestine leaves the stomach from the right side, anteriorly, and the caecum peculiar to the Pholadacea is present as a hemispherical rudiment on the right side, just posterior to the opening of the intestine.

The nervous system of the larva is highly specialized. The ganglia are composed of ganglion cells and the connectives contain only nerve-fibres. On either side the pleural ganglion is still separate from the cerebral. From the pleural a connective passes to the visceral, and from the cerebral, one to the pedal. I think a pleura-pedal connective is also present, but this I am not able to state positively. The two pedal ganglia are closely fused, while the visceral are wide apart.

The kidneys consist of large vacuolated cells, and open externally in front of the posterior adductor. The internal, pericardial openings I have not been able to find. Lying around the cerebral ganglion is a gland, which so far as known, is peculiar to "ship-worms" and which in later stages, becomes so greatly developed in connection with the gills. The glandular portion contains spherical cells, and from it a duct opens to the exterior under the cerebral ganglion.

METAMORPHOSIS.—The duration of the free-swimming life of the larva is not known, but it is perhaps a month, more or less. In a very much shorter period, the peculiar “ship-worm” has been developed, with adult organization. The first change is the sudden, complete loss of the velum. Within a few hours after the larva has settled, the velum begins to disintegrate, and its constituent cells are cast off and eaten by the larva. The lower lip is projected forwards under the cavity of the velum, and as the cells are cast off, they cannot pass to the exterior, and so are eaten. The basement membrane of the cells of the velum contracts rapidly and the cavity of the velum is very quickly obliterated (within a few hours).

Accompanying the loss of the velum, the long byssus thread has been secreted. As soon as the larva is secure, it seeks a place to burrow, and in preparation for its future life, its whole organization begins to change. The fusion of the mantle ventrally progresses rapidly, and within two or three days only the opening for the foot is left. The siphons elongate rapidly and very early; the mantle grows out so as to project beyond the shell. The latter changes rapidly after attachment. Within two days the first row of teeth has been formed on either valve; the greater growth on the ventral edges causes the two valves to gape for the protrusion of the foot; the knobs have been formed on dorsal and ventral portions; the apophyses have been formed and the retractor muscles of the foot have become attached to them. The foot, meanwhile, has become pestle-shaped.

The alimentary canal takes an important part in the general change. The caecum of the stomach, present in the larva as a rudiment, enlarges very rapidly, and even before woody material has been ingested in quantity, it projects as a large vesicle into the foot. In the early stage (4 days attached, a half millimeter long) it already forms a large part of a visceral mass. As the ingestion of woody materials progresses, the caecum projects more and more posteriorly, and in specimens 2 mm.

long, it extends much beyond the posterior adductor. The gills soon grow around the foot posteriorly and in specimens 2 mm. long, ten to twelve days old, project much beyond the visceral mass. This same stage also shows the pericardial space, with its contained and associated structures, in the position which it occupies in the adult, distinctly posterior to the large adductor. And, in this, as in subsequent stages the visceral ganglion lies on the posterior end of the pericardial cavity.

There are a number of facts in the organization and metamorphosis of the larva that seem to have a wider significance. One of these is the sudden and complete loss of the velum. Loven thought that, in forms studied by him, it entered into the formation of the labial palps. These structures are present in *X. fimbriata* only as the small ridges on the sides of a slight groove around the mouth; so that a form in which they may be said to be absent, does not give necessary evidence against the derivation of the palps from the velum in forms in which the former are well developed. However, the velum in various Lamellibranch larvae is very much larger than the palps in early stages, so that most of it must be cast off or absorbed. In the newly-attached oyster I have observed that the cells of the velum are absorbed more slowly, though the palps are developed somewhat later merely as ridges on the sides of the mouth. The evidence from *X. fimbriata* and *O. virginiana*, it seems to me, shows conclusively that the palps are not derived from the velum. The loss of the velum is an event not confined to the Lamellibranchs. Wilson (17) has observed that the trochal cells of *Polygordius* are suddenly cast off and eaten as in *X. fimbriata*, and Pruvot has described the loss of the test in *Dondessie*. These all seem to be one and the same phenomenon, and indicate that the loss of a part of the ectodermal covering in these and many other forms is a very primitive and general occurrence.

